

NOTES ON THE FROG GENUS *THOROPA*
(AMPHIBIA: LEPTODACTYLIDAE)
WITH A DESCRIPTION OF A NEW
SPECIES (*THOROPA SAXATILIS*)

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Abstract. — A new species of *Thoropa* (*T. saxatilis*) is described from the State of Santa Catarina, Brazil. This species and the two other large *Thoropa* occur allopatrically in the middle and southern Atlantic Forest Domain and campos rupestres of Brazil. The ranges of the two small *Thoropa* species overlap with each other and with *T. miliaris* in the middle Atlantic Forest region. Immunological microcomplement fixation albumin distances indicate that the large forms share a similar ancestral morphology and that distributions cannot be explained on the basis of recent allopatric speciation of a widespread ancestor. Adult male *Thoropa* have clusters of dark spines or a pad on the hand, and males of four out of five species either show scarring on the dorsum indicative of male combat or are reported to be territorial.

While preparing a description for a new species of *Thoropa*, we found considerable previously unpublished data on localities, natural history, and nomenclature of this genus. The purpose of this paper is to summarize these findings in addition to describing the new species.

Nomenclature

While reviewing previously proposed names for *Thoropa* to verify that the new species was undescribed, we encountered one locality citation and one synonymy worthy of comment.

As Cochran's work (1955) often serves as a starting reference for those interested in the frogs of southeast Brazil, an error in a type locality is worth pointing out. Cochran (1955:293) gives the type locality of *Cystignathus missiessii* Eydoux & Souleyet, 1842 (the type species of *Thoropa* Cope), as "Eijouja." The locality as it appears in Eydoux & Souleyet (1842:149) is "... Tijouka, aux environs de Rio-Janeiro." Bokermann (1966:33) gives the type locality correctly as Tijuca, Rio de Janeiro, without comment.

Cochran (1955:297) stated that "In Vienna I examined Fitzinger's type of *Eupsophus fuliginosus*, from Rio de Janeiro taken by the Novara Expedition, 1857-1859; it appears to be a young *E. miliaris*." She also presented a photograph of the type (plate 25, fig. E), for which the original photographs are still available (in our files). We disagree that *E. fuliginosus* is a synonym of *T. miliaris*. *Thoropa miliaris* typically has dark squarish or oblong dorsal blotches and distinct light markings on the posterior surface of the thigh (shown in Cochran's [1955] photograph of *T. miliaris*, plate 25, fig. F). The holotype of *E. fuliginosus* has a dark inverted V-shaped mark on the dorsum and the posterior surfaces of the thighs are almost uniformly dark, lacking distinct light marks. The dorsal pattern of the holotype of *E. fuliginosus* is the same as that found in individuals of *Thoropa lutzi* and *T. petropolitana* and differs from the dorsal patterns of both the new species and *T. megatympanum*. The finger tips of the holotype of *E. fuliginosus* are not swollen or expanded, as are those of *T. miliaris*, *T. lutzi*, and the new species. The second finger is longer

than the first in the holotype of *E. fuliginosus* and in *T. petropolitana*; the first finger is longer than the second in all but the smallest *T. miliaris* (15 mm SVL). The holotype of *E. fuliginosus* (23 mm SVL) is in poor condition and does not have any nuptial spines or pads on the thumb. Drs. Grillitsch and Tiedemann (pers. comm.) kindly examined the holotype for us and stated that they are "sure that this specimen is a male." As adult male *Thoropa* have either thumb pads or spines, their absence in the holotype suggests that they have fallen off, apparently due to preservation problems (this condition is seen, albeit rarely, in other *Thoropa* specimens). The pattern of the posterior surface of the thigh in the holotype (almost uniformly dark with a few light specks) does not match the pattern found in most *T. petropolitana* (mottled, with dark cross bars dorsally). Fitzinger (1861:414) gave the type locality of *E. fuliginosus* as "Brasilien." Gans (1955) indicated that the "Novara Reise" was only in the region of Rio de Janeiro in Brazil, but included Rio de Janeiro, Corcovado, Tijuca, and Petrópolis, localities from which *T. lutzi*, *miliaris*, and *petropolitana* have been collected.

In summary, the following characteristics of the holotype of *E. fuliginosus* argue for or are consistent with the synonymy of *T. petropolitana* with *E. fuliginosus*: locality, adult size, dorsal pattern, relative first and second finger lengths, and finger-tip condition. The following two features argue against the synonymy of *T. petropolitana* with *E. fuliginosus*: lack of thumb spines, and the pattern on the posterior thigh. In our opinion, *E. fuliginosus* is definitely not the same species as either *T. lutzi*, *megatympnum*, *miliaris*, or the new species. The relationship of *E. fuliginosus* to *T. petropolitana* will not be settled until the holotype of *E. fuliginosus* is examined by someone familiar with variation in all *Thoropa*. Since we are unable to examine the holotype, we cannot resolve the question of the potential synonymy of *T. petropolitana* with

E. fuliginosus; we consider *E. fuliginosus* a nomen dubium. We are certain, however, that neither *E. fuliginosus* nor any other name proposed for a *Thoropa* species applies to the new species, proposed as:

Thoropa saxatilis, new species

Fig. 1

Holotype.—MZUSP (Museu de Zoologia, Universidade de São Paulo) 64778, adult male, 23 Nov 1979, 20 km E of Bom Jardim on the road to Lauro Müller, State of Santa Catarina, Brazil, W. Ronald Heyer, Frances Irish, and Francisca C. do Val.

Paratopotypes.—MZUSP 35478–96 (juveniles), Gertrude Rita Kloss, between 25 Oct and 14 Dec 1970.

Description of holotype.—Snout rounded in profile, nearly rounded from above; nostrils lateral, near tip of snout; canthus rostralis indistinct; loreal obtuse; tympanum distinct, rounded, just larger than eye; prominent annular ring hidden dorsally by supratympanic fold, fold extending halfway down posterior edge of tympanum; tongue elongate with slight emargination on anterior edge; vomerine teeth forming an obtuse angle between anterior portion of choanae, separated by less than one choanal diameter; vocal slits and sac absent; finger lengths $\text{III} > \text{IV} > \text{II} = \text{I}$; fingers unwebbed but with lateral ridges; tips of fingers flattened, expanded, disk shaped, wider than long (disk on finger III 2.4 mm wide), finger disks much more pronounced than toe disks; palmar tubercle large, cordate; thenar tubercle large, merging with prepollex, forming a rounded triangle with apex on palm, separated from thumb subarticular tubercle by about one length of subarticular tubercle; one rounded subarticular tubercle on finger II, two on fingers III and IV; no supernumerary tubercles on fingers; several small, accessory palmar tubercles; cluster of dark spines on distal surface of prepollex, and on dorsal surface of thumb above second joint, extending nearly to disk; row of 11–12 spines

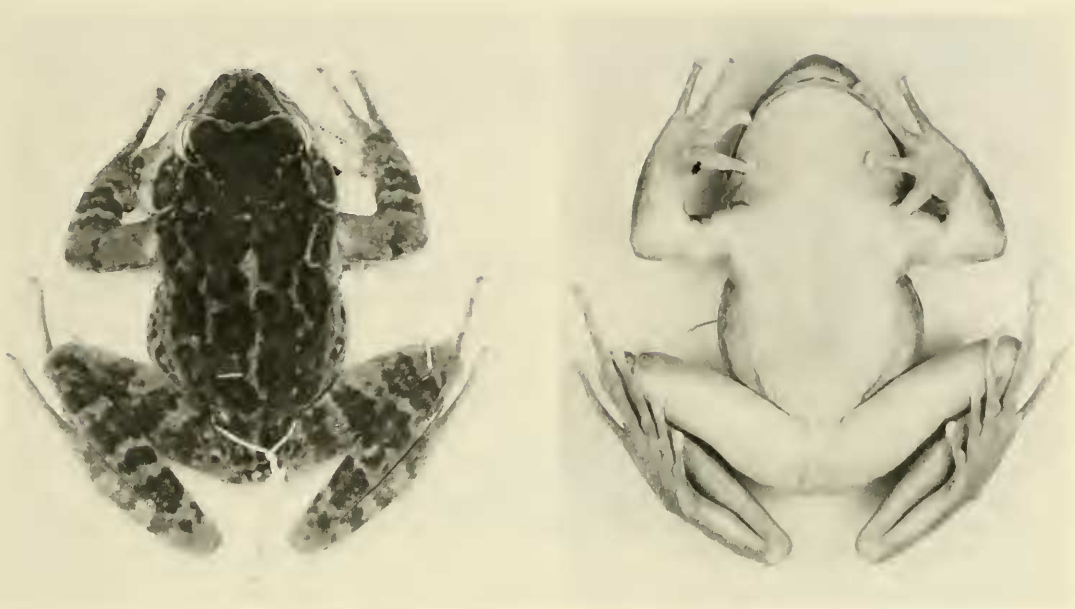


Fig. 1. Dorsal and ventral views of holotype of *Thoropa saxatilis*.

dorsally on inner side of finger II, and row of 4–6 spines on finger III; dorsal texture smooth (weakly crenulate under magnification), upper eyelid granular, numerous scattered, low warts on flanks; venter smooth, under surface of thighs granular; tips of toes slightly expanded, flattened; toes unwebbed but with lateral ridges, ridges most pronounced on outer edges and on toe III; elongate inner metatarsal tubercle larger than rounded, pungent, outer metatarsal tubercle; weak tarsal fold extending length of tarsus.

SVL 57.5 mm; head length 21.7 mm; head width 23.9 mm; horizontal tympanum diameter 6.5 mm (including annulus); eye diameter 6.1 mm; distance from eye to posterior edge of naris 6.2 mm; thigh length 30.5 mm; shank length 33.9 mm; foot length 33.1 mm.

In preservative, dorsal basal color dark brown, with scattered, small light brown patches and irregular, longitudinal light brown patches; flanks indistinctly mottled gray and brown with scattered, low, light-pigmented warts; light gray-brown inter-

ocular line with wavy margins; upper lip light brown at base, brown in places extending upward and merging with gray loreal color. Dark brown, relatively broad canthal stripe from in front of naris to eye; upper surfaces of limbs barred; posterior surface of thigh almost uniform light brown with a few scattered light flecks; venter cream with light brown wash, wash more concentrated on throat and pectoral region.

Variation in adult specimens (n = 2 males, USNM [collections in National Museum of Natural History, Smithsonian Institution] 245972–73).—In preservative, the dorsal color ranges from a dark and light brown mottle in one specimen to light gray mottled with indistinct, rounded dark gray patches, a light central blotch, and light flecking on flanks and behind eyes in the other. The loreal color ranges from light brown to gray, the upper lip from dark brown to gray. The dorsal texture is smooth with numerous low warts on flanks and/or posteriorly on dorsum. One or two light interocular bars (dark bordered in one specimen) are present. Asperities are present on thumb and finger II

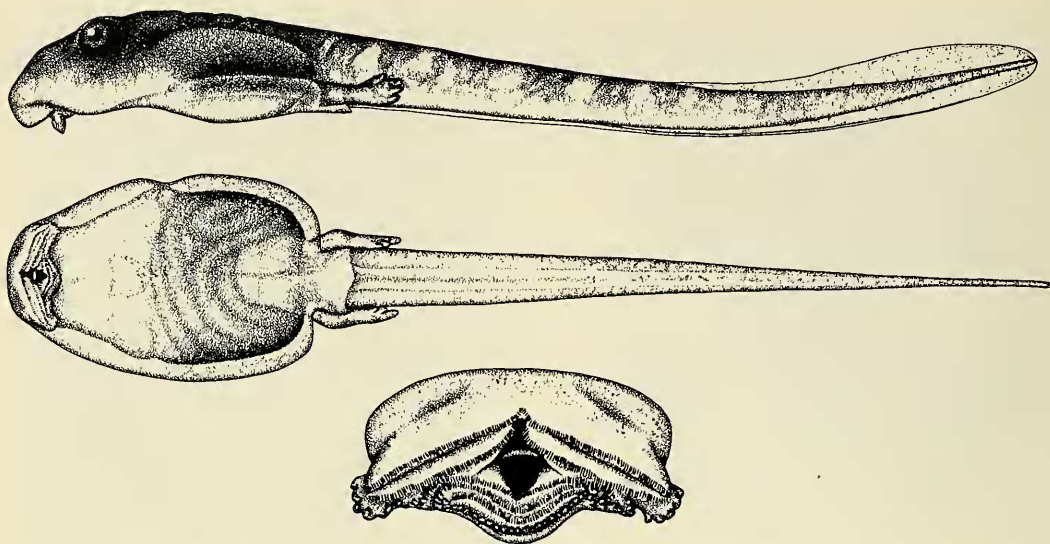


Fig. 2. Lateral, ventral, and mouthpart views of larval *Thoropa saxatilis*, stage 37.

or fingers II and III; the tympanum is just larger than the eye in one specimen and just smaller than the eye in the other. The disk on finger III is slightly more than twice the width of the finger at its narrowest point in one specimen, slightly less than twice the finger width in the other specimen.

Description of the larvae.—In addition to the specimen (stage 37) described and illustrated (Fig. 2), 10 other specimens (stages 29–39) were examined. The ranges of variation for these specimens appear in parentheses. Terminology follows Altig (1970).

Larvae elongate, depressed; tail fin low; dorsal fin present only on posterior 45% (35–60%) tail; ventral fin flattened and broadened, forming a concave strip narrowing posteriorly; depth of ventral fin increasing posteriorly, becoming just shallower than dorsal fin on posterior 40% of tail. Venter flattened, ventral skin forming a shelf extending slightly from the sides of the body, with a posterior flap projecting under the tail; spiracle sinistral, very small; anus median; eye moderately large, 15% (14–17%) head–body length; oral disk broad, 36% (34–41%) head–body length; oral disk laterally

indented; oral papillae in single row, continuous posteriorly, but with anterior gap almost width of disk; tooth row formula 2(2)/3(1); upper tooth row adjacent to beaks consisting of two separate rows abutting medially; beaks laterally compressed, with deep central cusps.

Total length 28.5 mm (16.9–33.9 mm); head–body length 29% (29–33%) total length.

Dorsal color brown, lightening posteriorly; tail barred dorsally with lighter brown. Gut visible through peritoneum and ventral skin, ventral surfaces unpigmented except for few scattered melanophores on belly and posterior tail.

Habitat.—Two adult males and all juveniles collected by Heyer and associates were taken in January, from 2000–2215, along roadcuts where a thin film of water trickled over steeply inclined or vertical rock faces; larvae were collected from the same habitat. One adult male (the holotype) was collected in November, between 2100 and 2215 hr, on a rock near a waterfall in a ½–1 m wide stream. All collecting sites were in primary or secondary forest.

Advertisement call.—The call of this species is unknown. Although *Thoropa* lack vocal slits or sacs, calls have been recorded or reported for the other four species in the genus.

Etymology.—*Saxatilis* is a Latin word meaning “found among rocks.”

Distribution (Fig. 4).—Southernmost extent of the Atlantic Forest and adjacent derivatives in the States of Santa Catarina and Rio Grande do Sul.

Referred specimens.—Brazil: Santa Catarina; Timbe do Sul (16 km from on road to Bom Jesus), USNM 245975–77, MZUSP 64786–93; Timbe do Sul (13 km from on road to Bom Jesus), USNM 245978–83; Itaimbezinho (10 km from on road to Praia Grande), USNM 245968–73, 245974 (larvae), MZUSP 64779–84, 64785 (larvae). Due to the high degree of local genetic differentiation of certain other Atlantic Forest frogs (e.g. Maxson & Heyer 1982), we feel it more prudent to consider other material we have examined from nearby localities as referred specimens, rather than type material.

Key to Adult *Thoropa* species

- 1. Finger disks markedly expanded, width of disk on finger III about twice width of finger at its narrowest point 2
 - Finger disks not or only slightly expanded 3
- 2. Tympanum in adults about 60% size of eye, annulus and supratympanic fold low and indistinct; adult SVL 22–28 mm (males), 30 mm (females); asperities in males two dense, rounded patches of minute spines on thumb *T. lutzi*
 - Tympanum in adults about 110% size of eye, annulus and supratympanic fold raised and distinct; adult SVL 41–58 mm (males); asperities in males in two patches of scattered spines on thumb and 1–2 rows on fingers II and III *T. saxatilis*

- 3. Posterior surface of thigh dark brown with contrasting, irregular, elongate white patches; dorsum often with 1–3 large, dark brown blotches (often with light borders) between eyes and sacrum *T. miliaris*
 - Posterior surface of thigh uniform brown with light flecks or light and dark brown mottle; dorsum mottled light and dark brown 4
- 4. Tympanum in adults 100–110% size of eye, annulus and supratympanic fold pronounced; finger I longer than finger II; adult SVL 32–51 mm (males), 38–49 mm (females); males with two patches of spines on thumb, 1–2 rows of spines on fingers II and III *T. megatympanum*
 - Tympanum in adults 60–70% size of eye, annulus and supratympanic fold low and indistinct; finger II longer than finger I; adult SVL 18–24 mm (males), 22–27 mm (females); males with a single patch of spines on thumb *T. petropolitana*

Key to Larval *Thoropa* species

- 1. Skin on belly forming a ventrolateral shelf or ridge extending out from sides of body 2
 - Skin on belly not forming a ventrolateral shelf or ridge extending out from sides of body *T. megatympanum*
- 2. Ventral skin shelf ending at posterior end of body, with posterior projection under tail 3
 - Ventral skin shelf extending, entire, past posterior end of body 4
- 3. Tail fin near tip of tail deeper than tail musculature, tip of tail rounded *T. saxatilis*
 - Tail fins near tip of tail less than or equal to depth of tail musculature, tip of tail tapering to a point *T. miliaris*
- 4. Belly transparent, viscera not or only

- slightly obscured by ventral musculature *T. lutzi*
 – Belly opaque, viscera obscured by
 sheet of ventral musculature
 *T. petropolitana*

Distribution

The known distribution of the genus *Thoropa* is concentrated in the middle and southern extent of the Atlantic Forests and the campos rupestres of the serras of Minas Gerais, with a few notable outliers (Fig. 3). One literature record not mapped (Fig. 3) is the type locality of *T. miliaris*, “fluminis Amazonum,” which has been considered as erroneous by several authors (e.g., Bokermann 1965). There are two other localities that may well be in error. The first is the type locality of *Hyloides brienii*, Itaeté, Bahia (de Witte 1930) (Fig. 3, northernmost triangle). We have not examined the holotype, but the photographs accompanying the original description are good and there is no reason to question the identity of the specimen as anything but *Thoropa miliaris*. Itaeté is far removed geographically from the nearest *T. miliaris* locality (Fig. 3) and although we are not familiar with the environs of Itaeté, it is unlikely that characteristic *Thoropa* habitat is found there. A similar problem of apparent locality error has been noted for *Melanophryniscus* from the same expedition (see Frost 1985:68). Two adult specimens of *T. miliaris* from the Museu Nacional (Rio de Janeiro) collection (41a, b) have the locality data of São Paulo, Cachoeira de Itú (=Salto, 23°12'S, 47°17'W, P. E. Vanzolini, pers. comm.) (Fig. 3, southernmost triangle). This locality is outside of the Atlantic Forests in the State of São Paulo. There are no specimens of *Thoropa* from the area around Salto in the MZUSP collections, which increases the likelihood that this locality is in error. As there is considerable doubt about these two *T. miliaris* localities, we exclude them from further analysis. The remaining problematic locality

(Fig. 3, remaining triangle in the State of Bahia) is a problem of identification. Miguel T. Rodrigues recently collected three very small *Thoropa* from Itajimirim, Bahia. The specimens clearly are *Thoropa*, but we are unable to assign them unequivocally to a species. They may represent a new species. If not, they are morphologically most similar to *T. megatympnum*; in any case, additional material is needed to clarify the identification. One additional noteworthy feature in the overall distribution of members of the genus *Thoropa* is the hiatus in the southeastern portion of the State of São Paulo, eastern Paraná, and north and central eastern Santa Catarina (Fig. 3). Within the middle and southern Atlantic Forests, *Thoropa* often share the same general habitat and usually are collected with members of the genus *Cycloramphus*. *Cycloramphus* species have been collected throughout the region of the distributional hiatus of *Thoropa* (Heyer 1983), so we believe this hiatus to be real and not an artifact of collecting.

The three large species of *Thoropa* are allopatrically distributed with respect to each other (Fig. 4). *Thoropa megatympnum* is now known from several localities in the State of Minas Gerais where campo rupestre vegetation is characteristic (see Giulietti & Pirani, 1988, for a discussion of campo rupestre) (Fig. 4, triangles). Morphologically, all populations appear similar. *Thoropa miliaris* is known from the Atlantic Forest and Atlantic Forest derivative vegetation in the States of Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo (Fig. 4). The question mark indicates a juvenile *Thoropa* (MZUSP 27250) with the locality “Serra da Bocaina.” The individual is a *Thoropa*, probably *miliaris*, but positive identification is precluded by the condition of the specimen. It is curious that this specimen represents the only *Thoropa* record from the Serra da Bocaina, where extensive frog collections have been made. There is morphological variation within the species recognized in this paper as *T. miliaris*, most

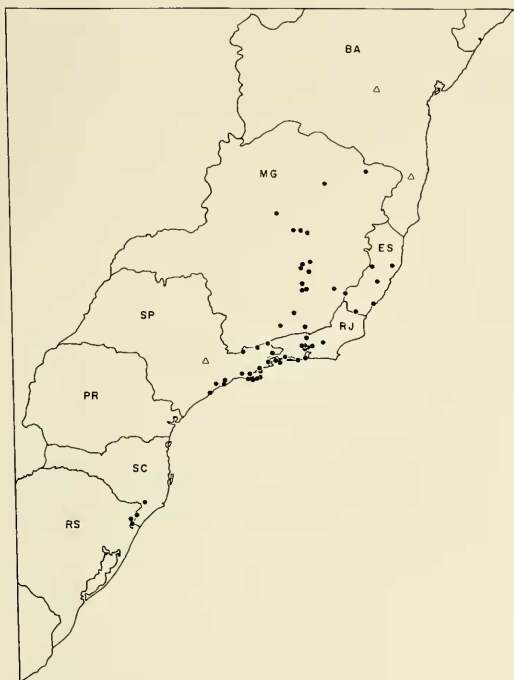


Fig. 3. Map of portion of eastern Brazil bounded by 10° and 55° W showing known and reported *Thoropa* localities. Triangles indicate questions of locality and identification (see text). State symbols: BA = Bahia; ES = Espírito Santo; MG = Minas Gerais; PR = Paraná; RJ = Rio de Janeiro; RS = Rio Grande do Sul.

notably in size; adults of the northern populations are notably smaller than those of the southern populations. Some of the variation is undoubtedly due to the presence of at least two cryptic species (see following section). *Thoropa saxatilis* is known from the southernmost extent of the Atlantic Forests in the State of Santa Catarina and possibly from a nearby locality in the State of Rio Grande do Sul. Braun & Braun (1980) record *Thoropa miliaris* from Cambará do Sul. Although we have not examined the specimen(s) in question, this record most likely refers to *T. saxatilis*. Bokermann (1965) tentatively included São Francisco de Paula, Rio Grande do Sul, as a *T. miliaris* locality, based on Hensel's (1867) report. Hensel (1867) used the name *Hylodes ab-*



Fig. 4. Distribution of large species of *Thoropa*. Open symbols indicate literature records for which we have not examined specimens. Triangles = *T. megalotympanum*, circles = *T. miliaris*, squares = *T. saxatilis*. Question mark indicates possible *T. miliaris* locality in Serra da Bocaina (see text). State symbols as in Fig. 3.

breviatus. We concur with Bokermann (1965) that Hensel likely had a *Thoropa* in hand (other authors have considered *Hyla abbreviata* Spix to be a *Thoropa*, but as Hoogmoed & Gruber (1983:359–361) point out, *H. abbreviata* is a synonym of *Eleutherodactylus binotatus*). Hensel did not give a specific locality for his *Hylodes abbreviatus* (= *Thoropa miliaris*) although he did state that the specimens came from sandstone holes in primary forest in Rio Grande do Sul. As no other *Thoropa* have been collected from anywhere near São Francisco de Paula (Braun & Braun 1980), we do not include this locality in the distribution of *T. saxatilis*.

The two small species of *Thoropa* are known from the same general areas in the States of Espírito Santo and Rio de Janeiro (Figs. 5, 6). The two species occur sympatrically at two localities: Santa Teresa, Espírito Santo, and Petrópolis, Rio de Janeiro. Three Museu Nacional specimens (3578) are



Fig. 5. Distribution of *Thoropa lutzi*. Open symbol indicates literature record for which we have not examined specimens. State symbols as in Fig. 3.



Fig. 6. Distribution of *Thoropa petropolitana*. Open circle indicates literature record for which we have not examined specimens. Triangle indicates questionable locality (see text). State symbol as in Fig. 3.

unquestionably *T. petropolitana* with the questionable locality data "Alto Serra de Cubatão ou Paranapiacaba, prope S. Paulo," collected by Hoge and B. Lutz, 17 December 1959. We also question this locality (Fig. 6, triangle) as these are the only specimens of *T. petropolitana* from the Cubatão-Paranapiacaba area, where extensive frog collections have been made, including large series of *T. miliaris*.

Thoropa megalotympanum and *T. saxatilis* are not known to occur sympatrically with any other *Thoropa* species. In contrast, at all localities where *T. lutzi* and/or *petropolitana* have been collected, *T. miliaris* has also been taken.

Relationships

Morphologically, the three large species (*T. megalotympanum*, *miliaris*, and *saxatilis*) are the most similar, not only in size but also in overall habitus and expression of male thumb and finger asperities. The distributions of these three species suggest recent allopatric speciation of a geographically widespread ancestor. However, the available data on estimates of genetic relatedness do not agree with this scenario. Maxson & Heyer (1982) reported immunologi-

cal microcomplement fixation albumin distance values (IDs) for certain *Thoropa*. Antisera were prepared for *T. miliaris* from Boracéia, São Paulo, and all distances are in reference to this population. *Thoropa miliaris* was closer to *T. lutzi* (ID = 16) and *petropolitana* (ID = 48) than to *megalotympanum* (ID = 60, listed as *T. sp.* in Maxson & Heyer 1982: table 3). Dr. Maxson kindly provided two additional values for inclusion in this paper. The available series of specimens of *T. miliaris* from Caparaó, on the state border of Espírito Santo and Minas Gerais, displays more pattern variation than typical *T. miliaris*, although some individuals do have patterns that are characteristic of *T. miliaris* elsewhere. Surprisingly, the ID value between the Boracéia and Caparaó samples is 37. The magnitude of this difference clearly indicates that the samples represent distinct species. We do not believe that presently available materials are adequate to separate the composite *T. miliaris*, however, and refrain from doing so.

The second value Dr. Maxson provided was between (Boracéia) *T. miliaris* and *T. saxatilis*, an ID value of 58. Although only one-way values are available, the data suggest that the overall similarities found among

the large *Thoropa* species are due to shared ancestral morphology, and that the speciation events among the larger species predate those leading to the smaller species. The available data suggest that detailed analyses of genetic estimates among *Thoropa* would be scientifically rewarding.

Territoriality and Male Combat in *Thoropa*

Shine (1979) suggested that where sexually dimorphic development of spines occurs in male anurans, it is an adaptation to combat between males, rather than to maintaining contact with females during amplexus. One of the most striking aspects of mature male *Thoropa* is the presence of clusters of dark spines on the inner portions of the hand. While examining specimens of *T. miliaris* from Boracéia we noted that most mature males had series of close-set, raking scratches on the dorsum, particularly behind the eyes and above the tympanum (Fig. 7). The configuration of the scratches is congruent with that of the spines on the thumb, prepollex, and fingers of adult male *T. miliaris* (see Bokermann 1965, fig. 5). Furthermore, these scratches occur on seven out of nine adult males but on none of the eight adult females or 23 juveniles examined in detail. We interpret this as evidence of male combat (see Kluge 1981, for a discussion of male combat and scarring from prepollical spines in *Hyla rosenbergi*). Although some scratches could have occurred in the bag after the specimens were collected, it seems unlikely that contact after capture played more than a minor role. Two of the males with extensive scratches were collected alone or with juveniles, so any scratches clearly occurred before capture. The remaining five males with scratches were collected in a series, so more than one male may have been in a single collecting bag. However, the scratches occur on five out of the six males and on none of three females in the series, and we were unable to detect any differences

in apparent age or placement of the marks between these males and the two mentioned above. Thus, we conclude that the scarring observed on these males resulted from face-to-face wrestling with other males at some point before they were collected.

Bokermann (1965) described the general ecology of three species of *Thoropa*. He reported that *T. miliaris* males show a marked tendency to occur in certain areas within their habitat on wet rock faces and to occupy a territory in which they feed and call. Females apparently are more wide-ranging, especially on rainy nights (Bokermann 1965).

Egg clutches of *T. miliaris* are deposited on wet rock faces near where males call and where the subaerial tadpoles subsequently develop (Myers 1946, Lutz 1954, Heyer & Crombie 1979). The length of the breeding season has not been reported for *T. miliaris*, but it appears to be a prolonged breeder in the sense of Wells (1977), with males calling for one to several months during the year (Heyer, pers. obs.). Where calling males occur, their density is low (Bokermann 1965; Heyer, pers. obs.). Non-breeding adults may feed in other habitats (Heyer, pers. obs.), so the territoriality of males on rock faces is probably primarily associated with reproduction. Suitable habitat for reproduction is available in man-made habitats such as quarry walls and road cuts, as well as natural rock outcrops. Even with the presence of man-made habitats, appropriate breeding habitat is probably a limited resource, as it almost certainly was in the forests where *Thoropa* evolved. Thus, it would be advantageous for a male to exclude other males from an area that would serve as a calling site, a potential egg deposition site, and suitable larval habitat.

The two other large species of *Thoropa* are *T. megatympanum* and *T. saxatilis*. Adult males of both species have spines very similar to those of *T. miliaris* (see Caramaschi & Sazima 1984:fig. 4, for *T. megatympanum*). Three out of four adult male *T. megatympanum* in the USNM collection

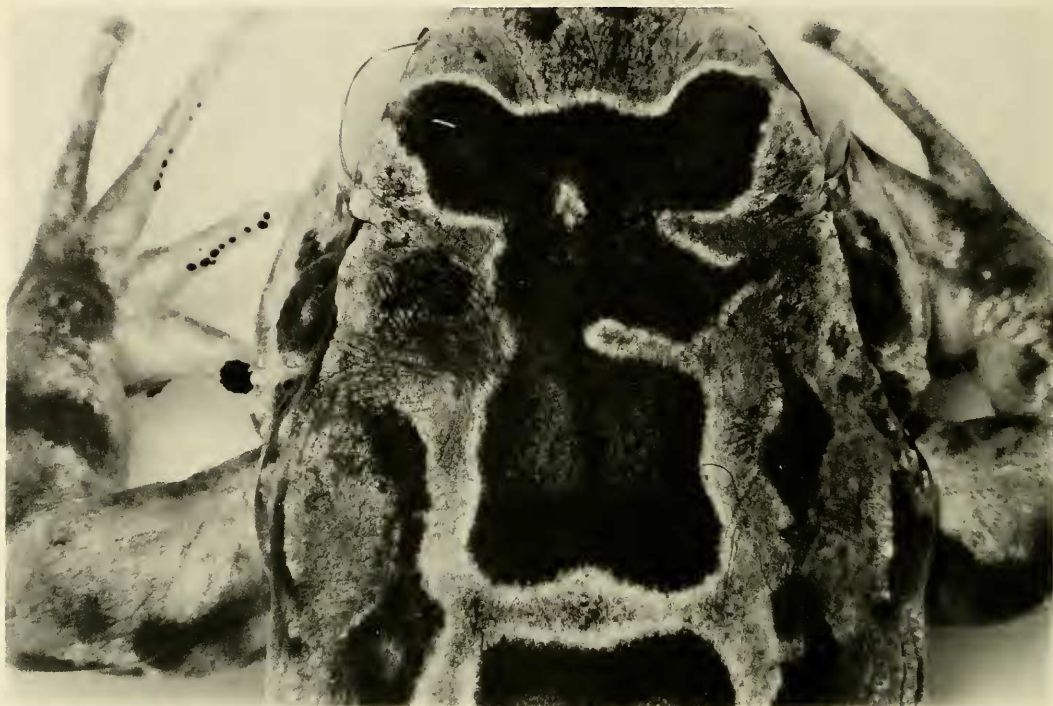


Fig. 7. Male *Thoropa miliaris* (USNM 209326) showing scratches on dorsal shoulder region.

have scratches similar to those found in *T. miliaris* (the remaining specimens, a male, two females, and a juvenile, lack scratches). *Thoropa megatympanum* breeds during the rainy season in the Serra do Cipó; males call from October to January and tadpoles have been found from November to February (Caramaschi & Sazima 1984). This species is found on inclined or vertical moist rock surfaces, under rocks, or in crevices on rocky, sandstone hillsides, and males call from hidden sites among the rocks (Caramaschi & Sazima 1984; Crombie, unpubl. data). Caramaschi & Sazima (1984) state that males are more "sedentary" than females; in conjunction with the evidence of male combat given above, this suggests that males are territorial and perhaps defend calling sites.

No information is available on the breeding behavior of *T. saxatilis*. All adults, juveniles, and tadpoles were collected on

roadcut rock walls with water seeping over the rocks or on a rock face near a waterfall. The largest of the three adult males collected shows, under a light microscope, two rake-like scratches on the dorsum, similar to those found in males of the other two large species. Given this evidence of male fighting and the similarities in habitat with *miliaris* and *megatympanum*, we predict that *T. saxatilis* is a prolonged-breeding species with territorial males.

Heyer & Crombie (1979) reported reproductive behavior in *T. petropolitana*, the smallest species in the genus. This species breeds for a month or longer (Bokermann 1965; Heyer, unpub. data) in areas where a film of water trickles over inclined or vertical rock faces. Males are territorial and defend calling and egg deposition sites against other males, with territorial calls, jerky posturing motions, and wrestling (Heyer & Crombie 1979). Although males

have a cluster of spines on the thumb which potentially could cause injury or scarring (see Bokermann 1965:fig. 7), we could find no corresponding marks on preserved specimens. Heyer & Crombie (1979) conclude that males are defending access to those limited sites providing appropriate conditions for egg deposition.

Few observations have been reported on the reproductive behavior of *T. lutzi*, the other small species in the genus. Males call on suitable wet rock wall habitat. Reproductive activity was recorded in January and February 1964 (Bokermann 1965), which suggests that this species also is a prolonged breeder. Males have two pads of minute spines on the thumb (see Bokermann 1965: fig. 6), but aggressive or territorial behavior has not been reported. However, since all the other members of the genus appear to be territorial, and since *T. lutzi* apparently is a prolonged breeder occurring in a limited breeding habitat, territoriality would not be unexpected.

Shine (1979) suggested that male combat was a selective pressure which could lead to large male size in frogs. Male combat apparently occurs in at least four of the five described species of *Thoropa*. However, females are larger than males in *T. miliaris* (Heyer et al., in press; Bokermann [1965] lists a snout-vent length of 78 mm for the largest male in his sample and 70 for the largest female, but does not provide means); *T. lutzi* (Bokermann 1965; Cocroft & Heyer, unpub. data); and *T. petropolitana* (Bokermann 1965; Cocroft & Heyer, unpub. data). Caramaschi & Sazima (1984) report that males are slightly larger than females in *T. megatympanum*, although data from 15 males and seven females in the MZUSP and USNM collections indicate that females are larger; in any case, the difference in size between the sexes is slight. No adult female *T. saxatilis* are available. Apparently, any selection pressure for large male size in *Thoropa* is balanced by pressures for large female size (see Woolbright 1983, Sullivan 1984).

Shine (1979) also suggested that combat is more likely to occur in the larger species within a group, since in large species males may face less risk of predation than in small species (we have encountered no evidence of toxicity in *Thoropa*, which could confer additional immunity from predation). However, it seems clear that male combat in *Thoropa* has arisen from life history traits unrelated to size, since it occurs in both large and small species. In *Thoropa*, male combat apparently has arisen as a means of territorial defense, giving males direct access to limited breeding sites occurring in the specialized habitat where the genus occurs.

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